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# Description of Three-New-Species of *Halgerda* from the Western Indian Ocean with a Redescription of *Halgerda formosa*, Bergh 1880

By

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Three new species of *Halgerda* are described from the tropical Indo-Pacific. *Halgerda dalanghita* sp. nov. is known from South Africa, Papua New Guinea and the Philippines. *Halgerda dichromis* sp. nov. is known from South Africa. *Halgerda toliara* sp. nov. is described from Madagascar. Comparison of the three new species is made with the original description and newly collected specimens of the type species, *Halgerda formosa* Bergh 1880 and other described members of the genus. The coloration, reproductive system and the radular morphology of these new species differ significantly from *H. formosa* and other previously described *Halgerda* species. Specimens of *Halgerda formosa* have been misidentified as *H. punctata* Farran, 1905 in recent literature and are compared here. Although these two species share some characteristics, they differ significantly in external and radular morphology.

Bergh (1880) introduced the genus *Halgerda* with the type species *Halgerda formosa*, based on a single specimen collected from La Reunion, and provided a description of the living animal based on the field notes of Dr. Koerbl, the collector. According to Bergh, the external coloration of this species is yellowish white with "orange-yellow stripes and black spots on its back, and black rhinophores" (Bergh 1880). Bergh described the preserved animal as having ridges which branch around the gills and rhinophores. His illustration of a second specimen from Mauritius (Bergh 1888, pl. 77, fig. 10) shows distinct dorsal ridges.

Farran (1905) introduced *Halgerda punctata* collected from Ceylon by Professor Herdman in 1902. Both Farran's description and illustration indicate large blunt tubercles arranged along the dorsum in a reticulate pattern. He also stated that in a second specimen, the ridges were "almost obsolete." Farran cited other differences between *H. punctata* and *H. formosa*. These differences included radular morphology, size and shape of both the foot and the anal papilla, and the number of gill branchia. Recent workers (Rudman 1978; Gosliner 1987; Wells and Bryce 1993) have suggested that *H. punctata* may be a synonym of *H. formosa*. The taxonomic relationships of these two nominal species are revised in the present study.

This paper describes three new species of *Halgerda*, which like *H. formosa*, are found in the Indian Ocean.

All material studied is deposited in The Natural History Museum of London (BMNH), the Department of Invertebrate Zoology and Geology of the California Academy of Sciences (CASIZ) and the South African Museum (SAM).

#### SPECIES DESCRIPTIONS

Family Halgerdidae Odhner, 1926 Genus *Halgerda* Bergh, 1880

TYPE SPECIES. — Halgerda formosa Bergh, 1880, by monotypy.

REMARKS. — Odhner (1926) introduced the family name Halgerdidae for *Halgerda*, and Thiele (1931) introduced Asteronotidae for *Asteronotus*. Odhner in Franc (1968) suggested that both family names are synonymous and included the genera *Aphelodoris*, *Halgerda*, *Sclerodoris* and *Asteronotus*. He employed Asteronotidae for the family despite the fact that Halgerdidae was used earlier and has priority. Others (Willan and Coleman 1984; Wells and Bryce 1993; Rudman 1998) have united most of the cryptobranch dorids into the single family Dorididae with or without employing a series of subfamilies. This approach unites more than sixty genera into a single unwieldy family which does not reflect phylogenetic relationships.

Since Halgerdidae is the older available name, we prefer to continue to place *Halgerda*, *Sclerodoris*, *Aphelodoris* and *Asteronotus* together in Halgerdidae, pending a complete phylogenetic analysis of the cryptobranch dorids.

# Halgerda formosa Bergh, 1880

Figs. 1A-B, 2, 3A

Halgerda formosa Bergh, 1880:190–195, pl. 4, figs. 15–20; pl. 5, figs. 10–12. 1888:822–826, pl. 77, figs. 10, 11; pl. 81, figs. 13–17.

Halgerda punctata Rudman, 1978:67, figs. 3A,7,8. misidentification; not H. punctata Farran, 1905.

Halgerda punctata Gosliner, 1987:69, middle photograph. misidentification; not *H. punctata* Farran, 1905. Halgerda punctata Wells and Bryce, 1993:106, top photograph. misidentification; not *H. punctata* Farran, 1905.

MATERIAL EXAMINED. — BMNH Reg. No. 1998027, Acc. No. 2350, one specimen, dissected, Grand Baic, Mauritius, 5 March 1990, H. Debelius. CASIZ 099340, one specimen, dissected, NE side Manahuanja Island, Msimbati, Mtwara Region, Southern Tanzania, 2 m depth, 4 November 1994, T. M. Gosliner.

DISTRIBUTION. — *Halgerda formosa* was originally described from Reunion Island (Bergh 1880), and later reported from Mauritius (Bergh 1888). Recent collections of specimens indicate that it is also found off Zanzibar (Rudman 1978), southern Tanzania (present study), Western Australia (Wells and Bryce 1993) and Sodwana Bay, South Africa (Gosliner 1987).

EXTERNAL MORPHOLOGY. — The preserved animals studied (CASIZ 099340 and BMNH 2350) measured 12 mm and 7 mm respectively. The body is firm and smooth, but rigid. The body profile is high and the dorsum has a series of low, angled ridges arranged in a reticulate pattern. There are no conical tubercles at the junctions of the ridges. The ground color of the dorsum and foot is whitish with a gray tinge. The ridges are lined with yellow-orange, with shorter, thinner yellow-orange lines in the depressions between the ridges on one specimen (CASIZ 099340) which are absent in the other. The ridges closest to the mantle margins have no yellow-orange coloration on them. There are small white tubercles along the mantle margin. The mantle edge has a thin, white line around the circumference. Along the edge of the mantle and on the foot are irregularly spaced, dark brown to black spots. The chocolate brown viscera can be seen through the translucent notum.

The upright rhinophores are tapered towards the tips, which have black coloration subapically. The black coloration extends down the posterior side of the translucent white rhinophores as a longitudinal band. There are 17 to 19 transverse rhinophoral lamellae on the animals included in the present study.

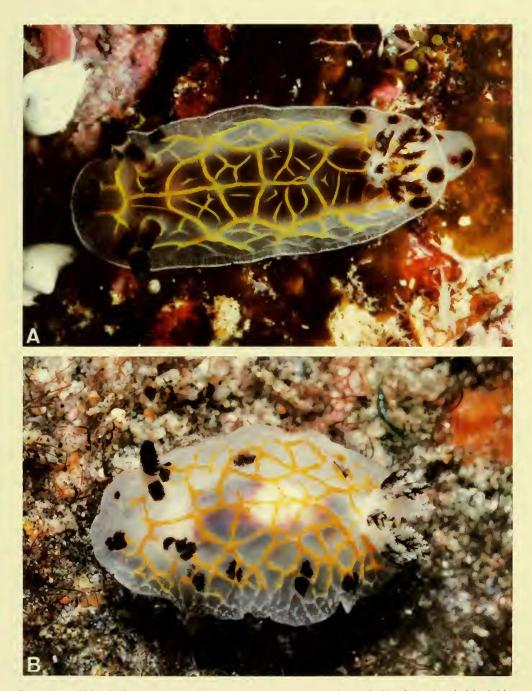


FIGURE 1. A. *Halgerda formosa* Bergh 1880 (CASIZ 099340). Specimen from NE side of Manahuanja Island, Mtwara Region, Tanzania, photograph by T. M. Gosliner, B. *Halgerda formosa* Bergh 1880. Specimen from Adlam's Reef, Sodwana Bay National Park, Natal, South Africa, photograph by T. M. Gosliner.

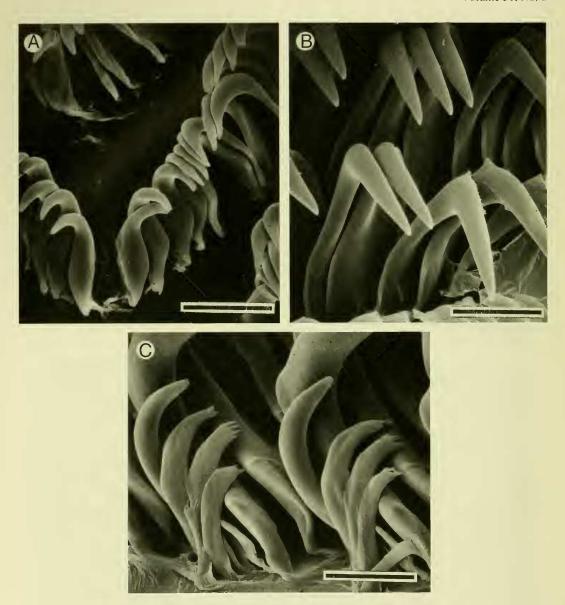


FIGURE 2. Halgerda formosa (CASIZ 099340). Scanning electron micrographs. A. Inner lateral teeth, scale =  $20 \mu m$ ; B. Middle lateral teeth, scale =  $43 \mu m$ ; C. Outer lateral teeth, scale =  $30 \mu m$ .

There are four tripinnate branchial leaves. The gills have black-lined branches and the pigment encircles each branch tip. Within the gill rachis are numerous flattened, translucent structures that appear glandular. The anal papilla is long and tubular with black coloration on both the posterior and anterior sides. The oral tentacles are short and digitiform. Some black spots on the ventral side of the foot are retained on the preserved animals.

BUCCAL ARMATURE. — The labial cuticle is smooth and devoid of rodlets. The radular sac is elongate, and the radular formula of one of the two dissected specimens is:  $36 \times 40.0.40$  (CASIZ 099340). The inner 7–8 lateral teeth are hamate although the hook is much shorter than that of the

middle lateral teeth (Fig. 2A). The middle lateral teeth are hamate with a rounded point on the crest (Fig. 2B). The 3 outer lateral teeth are modified with a series of fimbriate denticles (Fig. 2C).

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Fig. 3A). The ampulla is long and lies across the anterior of the female gland mass. The female gland mass is about the same size as the prostate gland. The ampulla narrows very slightly as it enters the postampullary duct and bifurcates into the vas deferens and oviduet. The short oviduet enters the female gland mass. The vas deferens separates from the ampulla and widens into the large, glandular prostate. The muscular portion of the vas deferens leaves the prostate in a long, single duct with one half-loop, then widens into the expansive penial bulb. The short uterine duct emerges from the female gland mass and joins the receptaculum seminis duct near its entry to the receptaculum. The receptaculum duct is long, convoluted and joins the oval receptaculum seminis with the larger, spherical bursa copulatrix adjacent to the vagina. The bursa is completely covered by the larger prostate. The vaginal duct, which emerges from the base of the bursa copulatrix, is short. There is a muscular sphincter at the entry to the vagina. The enlarged muscular region of the vagina constricts before its exit in the center of the genital atrium which has several deep fingerlike folds. Both the penis and the vagina are unarmed. The genital atrium is wide and large.

DISCUSSION. — Bergh (1880) described the 23-millimeter, type specimen of *Halgerda formosa* as having a white, high, oval body with a grayish tinge. The ridges were joined at two or three spots on the dorsum situated between the rhinophores and the gills. The ridges branched around the gills and rhinophores and continued to the mantle edge (Fig. 1A). Bergh (1880) reported the branches of the main ridges as yellowish in color, and in between the lateral ridges the bluish black coloration of the viscera could be seen. There were brownish black spots along the mantle edge. The wide stalks of the rhinophores were yellowish above the middle of the club, with coal black markings on the posterior surface, whereas the anterior of the stalk is whitish. He counted 25 rhinophoral lamellae. The small, tapering anal papilla was white with black markings on the inner surface, as were the stalks of the gill. The three branches of the gill also had black lines along their inner surface. The foot as described by Bergh (1880) and as found in the present study is fairly small and has black spots medially down the length.

Bergh's (1880) description of the radula included 51 rows of hooked teeth and 42–44 teeth per half-row. His drawings of the teeth of *H. formosa* show two denticulate outer lateral teeth. In addition, the radular sac as drawn (pl. 81, fig. 14) was long and curved.

Bergh presented a detailed description of the reproductive system. He reported that *H. formosa* has a large female gland mass, a prostate that covers the upper portion of the bursa copulatrix, a receptaculum seminis shaped like a compressed sphere and one-third to one-half the size of the bursa. There was no vaginal or penial armature. The penis was cylindrical and three times as thick as the sperm duct. The prostate had two distinct parts, one glandular and one long and snakelike that terminates into the penis. The uterine duct was long and the genital vestibule had long, deep folds.

A comparison of the specimens dissected in the present study (BMNH 2350, CASIZ 099340) to Bergh's (1880) description indicates that both are *Halgerda formosa* due to the following similar characters:

As with Bergh's descriptions of *Halgerda formosa*, both specimens examined have a series of low, angled ridges, with no tubercles at the junctions of the ridges. The ridges are lined with yellow-orange. The body color of the two specimens is white with a grayish tinge. Along the edge of the mantle and on the foot are irregularly spaced, dark brown to black spots. The rhinophores of the specimens, like *H. formosa* are tapered and have black coloration subapically. The gills have black-lined branches and the anal papilla is long and tubular with black coloration on both sides.

The specimen dissected (CASIZ 099349) has the same elongate radular sac and fimbriate (= denticulate of Bergh) outer denticles as described by Bergh for *Halgerda formosa*.

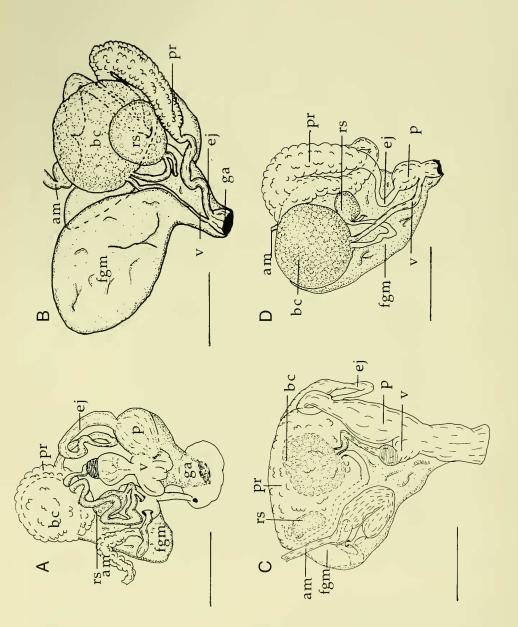


FIGURE 3. Reproductive systems with organs teased apart to show their arrangement, am = ampulla, bc = bursa copulatrix, ej = ejaculatory duct, figm = female gland mass, ga = genital atrium, p = penis, pr = prostate, rs = receptaculum seminis, v = vagina. A. Halgerda formosa. Scale = 1 mm. B. Halgerda dalanghita sp. nov. Scale = 2 mm. C. Halgerda dichromis sp. nov. Scale = 1.25 mm. D. Halgerda toliara sp. nov. Scale = 0.5 mm.

The reproductive system of both specimens (Fig. 3A) is as described by Bergh for *Halgerda formosa*. The penial bulb is large, as is the genital atrium. The large, glandular prostate covers the bursa copulatrix. The vaginal duct is short and emerges from the base of the bursa. Neither the vagina nor the penis are armed.

Yonow and Hayward (1991) examined the external morphology of the specimen (BMNH 2350) collected from Mauritius, and identified it as *Halgerda formosa*. Although no reproductive morphology is described in Yonow and Hayward's paper, the dissection was made in the present study, and there is little doubt that the specimen is indeed *H. formosa*. The external morphology described by Yonow and Hayward is nearly identical to Bergh's (1880) description of *Halgerda formosa*. The reproductive morphology of this specimen, examined for this study, is also identical to Bergh's description.

Farran (1905) placed *Halgerda punctata* in the genus *Halgerda* based on the following features: a smooth, leathery mantle with raised tubercular ridges, a bi-lipped foot, small tentacles which in *H. punctata* are tuberculate, a small number of branchial leaves, absence of jaws, a long curved radular sac, outer lateral teeth not denticulate and innermost teeth smaller. There were 50 rows of hooked teeth, with 50 teeth per each side of the row. There were no rachidian teeth and the penis and vagina were unarmed.

Farran (1905) described the mantle of *Halgerda punctata* as being white with numerous tubercles, which have a pinkish tinge on some of the apices. He noted that these tubercles were "more or less connected by ridges in a triangular network." Both the mantle and the ventral side of the animals he studied had a few black spots. The notes sent with the specimens from Professor Herdman, the collector, included mention of yellow papillae on the mantle and purple spots on the foot, with a few spots of the same color on the mantle. Farran described the anal papilla as long and tubular, white with a black scalloped margin.

Farran's (1905) work comparing Bergh's specimens of *Halgerda formosa* with *H. punctata* confirmed Bergh's original description of *H. formosa* that noted numerous dorsal ridges, crimson spots and yellow lines. The above external differences, along with the denticulate outer lateral teeth of *H. formosa*, as opposed to smooth ones in *H. punctata*, were the only differences Farran noted between the two species. Farran's illustration (pl. 3, fig. 4, ) of *H. punctata* is markedly different from Bergh's drawing of *H. formosa* in that Farran drew distinctive tubercles connected by low ridges along the high body profile, whereas Bergh drew distinctive ridges with no tubercles at all on a low body profile.

Rudman (1978) examined a specimen of *Halgerda* from Zanzibar and identified it as *Halgerda* punctata Farran. The animal he described had distinct ridges with bright lemon yellow angles and purple spots on the foot with few on the mantle. Rudman did not describe tubercles on this specimen, although in his discussion he mentioned that his specimen was identical to Bergh's *H. formosa*, including the "yellow papillae" on the mantle (Rudman 1978). Rudman described the radula as having smaller inner teeth and smooth, outer lateral teeth. Rudman's illustration of the radular sac indicates that it is long.

Rudman described the ejaculatory duct of the Zanzibar specimen as large, muscular and separate from the vagina, and the vagina as a thin-walled bulb with a muscular sphincter at the opening of the thin-walled vaginal duct as in our specimens of *H. formosa*.

Due to the external morphological similarities between Rudman's *Halgerda punctata* and Bergh's description of *H. formosa*, it appears that Rudman's (1978) specimen was actually *H. formosa*. Although the outer lateral teeth in *H. formosa* are drawn and described as denticulate (Bergh 1880), and Rudman's specimen are non-denticulate, radular variations within species are noted in other recent studies of *Halgerda* (Bertsch and Johnson 1982; Gosliner and Fahey 1998).

Gosliner (1987) described a specimen from South Africa also as *Halgerda punctata* that was similar to the Zanzibar specimen Rudman examined and identified as *H. punctata*. Gosliner described

Volume 51, No. 8

a translucent white color, plum colored spots on the notum, and yellow-orange ridges. Color slides of animals (Figs. 1A, B) collected in Zanzibar and Tanzania show the spots to be arranged along the mantle edge. While the specimen from South Africa has spots all along the mantle edge, the Tanzanian specimen has only five spots arranged asymmetrically on its posterior end, four spots on the anterior mantle edge, with two next to the rhinophores, and two on the extreme front. No tubercles are present on the notum of any *Halgerda* collected by Gosliner from South Africa. Based on the consistent characters between *H. formosa* and Gosliner's (1987) specimen, we have determined that Gosliner's specimen is most likely *H. formosa*.

Wells and Bryce (1993) illustrated a *Halgerda* specimen collected from Bundegi Reef, North West Cape of Australia, as *Halgerda punctata*. However, the animal pictured in that work has the identical, external morphological characteristics of *H. formosa* as described by Bergh (1880). This includes yellow-lined, low ridges, tubular anal papilla with dark pigment on the anterior side, black markings on the rhinophores, notum and gills. The gills also have black lines along their inner surface rather than black spots. No reproductive anatomy is described.

Based upon a comparison with Bergh's (1880) original description of *Halgerda formosa* and Farran's (1905) original description of *H. punctata*, Rudman's, Gosliner's and Wells and Bryce's specimens should have all been identified as *H. formosa*, not *H. punctata*.

Debelius (1996:254, bottom photo) described an animal collected from Sri Lanka whose external morphology is nearly identical to *Halgerda punctata* (Farran 1905). For example, the animal has blunt, yellow tubercles, some with pink apices. There are dark spots on the notum, arranged somewhat symmetrically. The rhinophores appear as described by Farran (1905): stout with black tips and thick white bases. The four branchia also match Farran's description as being thick with the anterior pair larger than the posterior pair, and black on the interior, but white on the outside. Debelius did not describe the reproductive or radular morphology of the specimen. We suggest that the specimen pictured in Debelius (1996) is *H. punctata*. The animal was not collected and could not be examined for the present study.

Rudman (1978) suggested that *H. punctata* may be a synonym of *H. formosa*. However, it appears from the morphological differences noted in the present study, that these are two distinct species, despite the fact that the reproductive anatomy of *H. punctata* has not been presented. Those distinctions are:

- *Halgerda formosa* has distinct low ridges lined in yellow to yellow-orange. *Halgerda punctata* has yellow tubercles. In *H. punctata*, the ridges are indistinct.
- Halgerda formosa has three, thick, main gill branches with the two lateral branches forked. The black coloration wraps around the gill from approximately halfway up the rachis. Halgerda punctata has four gill branches with the anterior two larger than the posterior pair. The gills have black margins on the interior and are white on the outside. The black pigment covers the entire length of each gill branch.
- The oral tentacles of *H. formosa* are short and digitiform. The tentacles of *H. punctata* are very small and tubercular (Farran 1905).
- The anal papilla of *H. formosa* is squat and tapering with black marks on the inner surface. The anal papilla of *H. punctata* is long and tubular with a black scalloped margin.
- *Halgerda formosa* has a thin foot; approximately one-fourth to one-third the width of the mantle. *Halgerda punctata* has a moderately wide foot (Farran 1905).
- The radular formula of *H. formosa* is  $51 \times 42.0.42$  (Bergh 1880),  $65 \times 64.0.64$  (Rudman 1978) and  $36 \times 40.0.40$  (present study), with the outer two lateral teeth denticulate (Bergh 1880; present study) or smooth (Rudman 1978). The radular formula of *H. punctata* is  $50 \times 50.0.50$  and the three outermost teeth are small and smooth.

• The innermost teeth of *Halgerda formosa* have large developed hooks and the four outer teeth are markedly smaller than the middle teeth. The 20 innermost teeth of *H. punctata* are very small and gradually increase in size towards the middle lateral teeth.

Halgerda dalanghita sp. nov.

Figs. 3B, 4A, 5, 6

Sclerodoris sp. Gosliner, 1987:68, top photograph.

TYPE MATERIAL. — HOLOTYPE: CASIZ 114775, Bethlehem, Maricaban Island, Batangas Province, Luzon, Philippines, 15 m depth, 24 April 1997, T. M. Gosliner. PARATYPES: CASIZ 110373, two specimens, one dissected, Bethlehem, Maricaban Island, Batangas Province, Luzon, Philippines, 15 m depth, 24 April 1997, T. M. Gosliner. CASIZ 111301, two specimens, one dissected, Anemone Reef, Papua New Guinea, 20 m depth, 22 February 1992, T. M. Gosliner. SAM A35416, one specimen, dissected, Mbibi, South Africa, 5 m depth, 8 May 1982, T. M. Gosliner. SAM A35410, one specimen, dissected, Mbibi, South Africa, 5 m depth, 6 May 1981, T. M. Gosliner. SAM A35415, one specimen, dissected, Adlam's Reef, Sodwana Bay, Natal, South Africa. 2 m depth, 9 May 1982. T. M. Gosliner.

DISTRIBUTION. — This species is known from Natal, South Africa, Papua New Guinea and the Philippines (present study).

ETYMOLOGY. — Halgerda dalanghita, is named for the color of the animals. Dalanghita is the

Tagalog word for a small orange fruit.

NATURAL HISTORY. — Halgerda dalanghita is found crawling in the open in shallow water, on near-shore reefs, rocky surfaces and also under coral rubble. It feeds on unidentified orange sponges and has been found from 5–20 m in depth. The three specimens from the Philippines were almost entirely embedded in a lobate orange sponge on which they had been feeding.

EXTERNAL MORPHOLOGY. — The preserved animals studied are 15–28 mm in length. The body is firm and smooth, like gelatin, but rigid. The body profile is relatively low and the dorsum has a series of angled ridges arranged in a reticulate pattern. There are no conical tubercles at the junctions of the ridges, as is present in some other *Halgerda* species. The ground color of the dorsum and foot is lemon yellow to orange. The ridges are lined in white, with additional short lines or dots of white sprinkled on the dorsum among the ridges. Brown dots, which outline the ridges and are scattered along the mantle edge, can be seen on some of the yellow to pale orange specimens. These brown spots are not present on one of the specimens from the Philippines. The pinkish viscera can be seen through the notum in the paler colored living animals.

The upright rhinophores are tapered towards the tip with brown coloration on the posterior side near the base, black subapical coloration and a translucent white background color. There are 17–18 rhinophoral lamellae.

The six branchial leaves are highly pinnate. The gills have black-lined branches, and the undersides are white. The pigment completely encircles each branch. Within the finely divided pinnate portion of the gill rachis, near the apices, are numerous flattened, translucent structures that appear glandular. The anal papilla is orange.

The oral tentacles are long and tapered outwards and posteriorly. Some light brown pigment spots on the ventral side of the mantle, near the margins of the foot, are retained on the preserved animals.

BUCCAL ARMATURE. — The buccal mass is not pigmented. The radular sac is short. The radular formulae of the five dissected specimens are:  $42 \times 33.0.33$  (CASIZ 110373) (Fig. 5),  $34 \times 29.0.29$  (SAM A35415),  $35 \times 25.0.25$  (SAM A35410),  $26 \times 27.0.27$  (SAM A35416) (Fig. 6) and  $35 \times 22.0.22$  (CASIZ 111301). The outer and middle lateral teeth are extremely elongate, which is atypical of dorid hamate teeth. It was difficult to confirm the radula formulae due to the teeth being extremely narrow,

numerous and irregularly arranged (Fig. 5B, D). The 5 or so inner lateral teeth are hamate (Fig. 6A, B).

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Fig. 3B). The wide ampulla is flattened and lies tightly against the female gland mass. The female gland mass is much larger than the prostate gland. The ampulla narrows into the postampullary duct, which bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The short vas deferens separates from the ampulla and widens into the large, elongate glandular prostate. The prostate consists of two distinct glandular types but they are not as well differentiated as in other members of *Halgerda*, but are differentially pigmented on all material examined. The muscular portion of the vas deferens leaves the prostate in a long, single duct with one half-loop, then widens slightly into the penial bulb. The short uterine duct emerges from the female gland mass and joins the receptaculum seminis near its base. The duct connecting the receptaculum and the bursa is moderately long. The pyriform receptaculum seminis is equal to or much smaller than the spherical bursa copulatrix. The bursa is not covered by the larger prostate. The receptaculum is partially hidden under the bursa and is also slightly tucked under the prostate. The vaginal duct that emerges from the base of the bursa copulatrix is long and thin. At its exit adjacent to the base of the male aperture, is an enlarged, but undivided portion that is not obviously glandular. The genital aperture is wide and large.

DISCUSSION. — Gosliner (1987) placed this species in the genus *Sclerodoris* Eliot, 1904. However, the type species, *S. tuberculata* Eliot, 1904 possesses a notum with caryophyllidia and broad outer teeth (Rudman 1978). The reproductive system of *S. tuberculata* also contains a distinct vestibular gland. As in other species of *Halgerda*, the present species has a smooth notal texture, narrow outer teeth and lacks a vestibular gland. Also, it has elongate rhinophores with black pigment, ridges that are of a different color than the body and opaque white gill glands, as in other species of *Halgerda*. *Halgerda dalanghita* is the only species of *Halgerda* with an orange general body color with varied pigment on the notum. The middle and outer lateral teeth of the radula of *H. dalanghita* are thin and elongate. The only other record of a *Halgerda* with similar radular teeth is that of Gosliner and Fahey (1998). In this case, some specimens of *H. elegans* Bergh, 1905 have elongate teeth while others have typical hamate teeth. All specimens of *H. dalanghita* examined here had elongate teeth. The radula sac of *H. dalanghita* is unique in being short, although all other described species of *Halgerda* have an extremely elongate sac.

The reproductive system of *H. dalanghita* has several distinctive features. The prostate does not cover the bursa copulatrix and is far less obviously differentiated into two distinct portions. However, the prostate does have two distinct gland types that are differentially pigmented in all preserved material examined. The vaginal and ejaculatory ducts are elongate and thin throughout their length.

# Halgerda dichromis sp. nov.

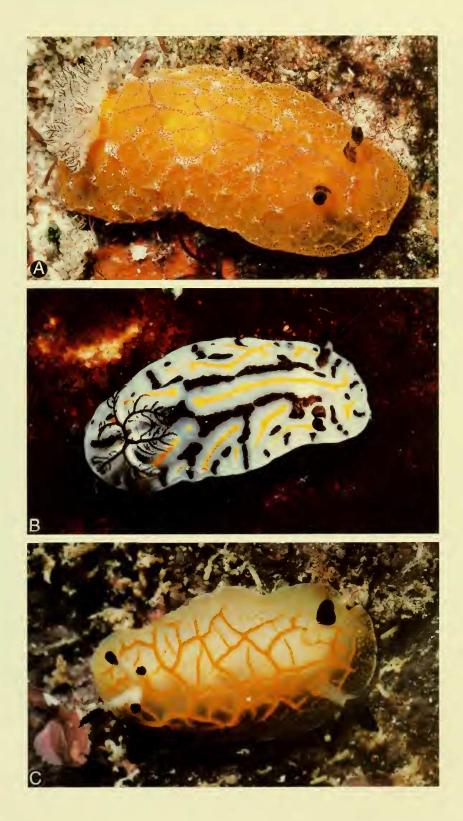
Figs. 3C, 4B, 7

Halgerda formosa Gosliner, 1987:69, top photograph, misidentification; not H. formosa Bergh, 1880.

TYPE MATERIAL. — HOLOTYPE: SAM A35413, one specimen, dissected, Vetchie's Pier, Durban Harbor, Natal, South Africa, 5 m depth, July 1980, W. R. Liltved.

 $\rightarrow$ 

FIGURE 4. A. *Halgerda dalanghita* sp. nov. (SAM A35415). Specimen from Adlam's Reef, Sodwana Bay, Natal, South Africa, photograph by T. M. Gosliner; B. *Halgerda dichromis* sp. nov. (SAM A35413). Specimen from Vetchie's Pier, Durban Harbor, South Africa, photograph by T. M. Gosliner; C. *Halgerda toliara* sp. nov. (CASIZ 111302). Specimen from 5 km SW of Mora Mora, Madagascar, photograph by T. M. Gosliner.



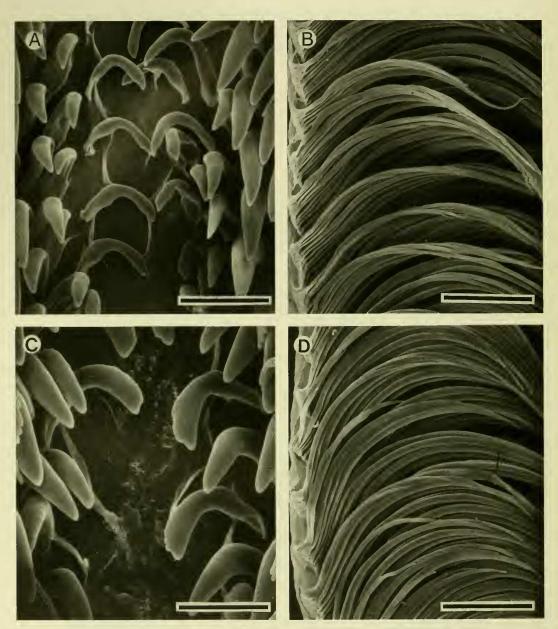


FIGURE 5. Halgerda dalanghita sp. nov. (CASIZ 110373) Bethlehem, Batangas Province, Philippines. Scanning electron micrographs. A. Inner lateral teeth, scale =  $60 \mu m$ ; B. Outer lateral teeth, scale =  $75 \mu m$ ; C. Close up of inner lateral teeth, scale =  $30 \mu m$ ; D. Outer lateral teeth, scale =  $60 \mu m$ .

ETYMOLOGY. — *Halgerda dichromis* is named to distinguish its bicolored ridges as compared to other *Halgerda* species, which have only one color on their ridges.

DISTRIBUTION. — The single specimen of *Halgerda dichromis* was found at the entrance to Durban Harbor in South Africa.

NATURAL HISTORY. — Halgerda dichromis is found in shallow sub-tropical water.

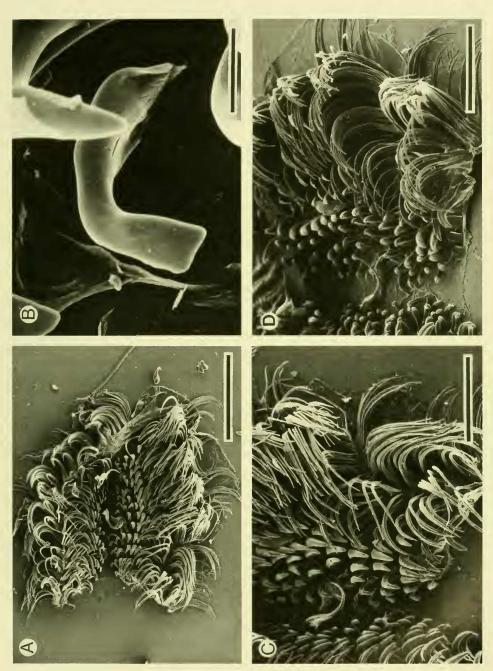


Figure 6. Halgerda dalamphita sp. nov. (SAM A35416) Mbibi, South Africa. Scanning electron micrographs. A. Radula, scale = 400 μm; B. Close-up of inner lateral teeth, scale = 20 μm; C. Radula, scale = 200 μm.

Volume 51, No. 8

EXTERNAL MORPHOLOGY. — The preserved animal is 16 mm in length. The living animal has an oval body that is firm, smooth and rigid. Although the body profile is slightly arched, this species does not have the high body form common in most other Halgerda. There are no tubercles at the junctions of the low, insignificant ridges. The ground color of the dorsum is grayish white, and the brown viscera can be seen through the skin of the notum. There is one thick orange line extending longitudinally along the notal midline. This orange line begins in front of the rhinophores and ends two-thirds of the way to the gill. On either side of this orange line are two heavy, equally-spaced black lines, which begin at the base of the rhinophores. They converge behind the orange midline, and continue as one black line up to and past the gill. There are shorter orange and black lines that form a reticulate pattern on the notum. Small black spots are found at the mantle edge both posteriorly and anteriorly.

The stocky rhinophores are angled posteriorly and have black coloration on their base posteriorly and also at the tips where the color encircles the club. There is a small white patch on the club approximately two-thirds of the way up its length.

The low, spreading gill has two lateral branches, each tripinnate. The two anterior branches are larger and more finely divided than the two posterior branches. There is a black ridge line on top of each branch. The underside of the gill is white. The same flattened, glandular structures reported previously in other *Halgerda* (Gosliner and Fahey 1998; present study) can be seen inside each gill rachis.

The anal papilla is short and stocky with black markings on the anterior side.

BUCCAL ARMATURE. — Since the radula is elongate, it is assumed that the radular sac was also, but this was not verified as the buccal mass was not available for this study. The labial cuticle is smooth and devoid of denticles. The radular formula of the holotype is  $48 \times 41.0.41$  (Fig. 7). The first twenty teeth are much smaller than the middle and outer lateral teeth, which gradually increase in size towards the outer edge. The outer three teeth are fimbriate in some rows but simply pointed in others.

REPRODUCTIVE SYSTEM. — The reproductive system (Fig. 3C) is triaulic. The ampulla is long and widens as it curves against the anterior of the female gland mass. It narrows and bifurcates into the vas deferens and oviduct. The massive prostate has two distinct glandular parts. The female gland mass is approximately the same size as the prostate gland. The muscular portion of the vas deferens leaves the prostate in a long, single duct with two half-loops, then widens into the large penial bulb. The short uterine duct emerges from the female gland mass and joins the receptaculum seminis near its base. The duct joining the receptaculum and bursa is long and joins the pyriform receptaculum seminis with the much larger, spherical bursa copulatrix adjacent to the vagina. The bursa is completely covered by the much larger prostate. The vaginal duct, which emerges from the base of the bursa copulatrix, is short relative to other species (Fig. 3). It narrows for most of its length but widens into a short muscular portion and a larger glandular portion near its exit adjacent to the base of the male aperture. Near the genital atrium, the vagina is large, muscular and bulbous, but not obviously glandular. Both the penis and the vagina are unarmed. The genital atrium is wide, large and elongate.

DISCUSSION. — Gosliner (1987) misidentified this specimen as Halgerda formosa, the type species of the genus, due to certain similarities. Both animals have a grayish white background color with yellow-orange ridges. Neither have tubercles at the ridge junctures and both have stocky rhinophores with black pigmentation. There are small black spots at the mantle edge of both animals and the gills are low and spreading with black pigmentation on the main branches.

Examination of the specimen from South Africa, and comparison to Bergh's 1880 and 1888 descriptions of Halgerda formosa indicate that the South African specimen should be regarded as a distinct species, H. dichromis.

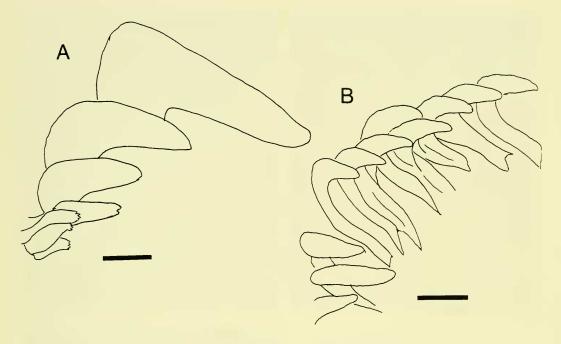


FIGURE 7. Halgerda dichromis sp. nov. Radular morphology. A. Outer lateral teeth, scale =  $40 \mu m$ ; B. Inner and middle lateral teeth, scale =  $400 \mu m$ .

The following differences are noted between *Halgerda formosa* and *H. dichromis*:

- 1) *Halgerda formosa* has distinct ridges lined in yellow, while *H. dichromis* has indistinct ridges and both black and yellow-orange lines on the notum.
- 2) The gills of *Halgerda formosa* are erect when fully extended, whereas the gills of *H. dichromis* are spread to form a flat gill.
- 3) *Halgerda formosa* has a distinct muscular sphincter at the point where the vagina widens prior to entering the genital atrium, whereas *H. dichromis* has no sphincter.
- 4) *Halgerda formosa* has a prostate that only covers the bursa copulatrix. The prostate of *H. dichromis* completely envelops the bursa, the anterior portion of the receptaculum and the oviduct.
- 5) The ejaculatory duct of *Halgerda formosa* is long, slender and terminates into a bulbous penis. The penis has a separate opening that terminates near the center of the wide genital atrium. The ejaculatory duct of *H. dichromis* is wide, then narrows before it terminates into a large, bulbous penis which itself terminates into a very long, wide genital atrium.
- 6) *Halgerda formosa* has a radular formula of  $51 \times 42.0.42$  (Bergh 1880),  $65 \times 64.0.64$  (Rudman 1978) and  $36 \times 40.0.40$  (present study), whereas *H. dichromis* has a formula of  $48 \times 41.0.41$ .
- 7) Halgerda dichromis has the inner 20 teeth much smaller than subsequent ones. Halgerda formosa has the inner 7–8 teeth smaller than the middle lateral teeth.
- 8) The gills of *H. dichromis* have a black medial line along the entire length of the gill as in *H. wasiniensis* Eliot, 1904 (Gosliner 1987:68, bottom photo) while in *H. formosa*, black pigment is restricted to the apices of the gill branches.

Although some of the external characteristics of *Halgerda dichromis* are similar to those of *H. formosa*, the two are clearly different species. Since many of the characteristics of *H. dichromis* are similar to other members of the *Halgerda* genus, a testable hypothesis of phylogeny is needed to determine how closely the species are related.

Halgerda toliara sp. nov.

Figs. 3D, 4C, 8

TYPE MATERIAL. — HOLOTYPE: CASIZ 111302, one specimen, 5 kilometers west of Mora Mora, Madagascar, 2 m depth, 7 April 1989, T. M. Gosliner. PARATYPES: CASIZ 073278, one specimen, off Soanambo Hotel, Ile Saint Marie, Madagascar, 2 m depth, 4 April 1990, T. M. Gosliner. CASIZ 073272, 2 specimens, one dissected, Patch Reef, Mora Mora, Madagascar, 2 m depth, 27 March 1990, T. M. Gosliner.

ETYMOLOGY. — *Toliara* is the Malagasy name for the Tulear region of Madagascar, where this species was first collected.

DISTRIBUTION. — *Halgerda toliara* has been found on both the west and east coasts of Madagascar (present study).

NATURAL HISTORY. — *Halgerda toliara* was found crawling in the open in shallow water on coral rubble.

EXTERNAL MORPHOLOGY. — The preserved animals are 9 mm (CASIZ 073272 and CASIZ 111300) and 5 mm (CASIZ 073278). The relatively low-profiled body is oval and the texture is smooth and firm. The ground color of the living animal is white to pale yellow-white. The white viscera can be seen through the notum of the living animals. There are low but distinct ridges arranged in a reticulate pattern on the dorsum. There are no tubercles at the junctions of the orange-lined ridges. Small yellow tubercles are scattered densely along the mantle margin. There is a thin white border along the mantle edge.

The long rhinophores have a base that is narrower than the top one-third of the club. The black coloration is found only at the top one-third, and it encircles the club. The bottom two-thirds of the rhinophores is translucent white.

The large gill has four sparsely pinnate branches, with the posterior pair divided into two on the paler colored animals. Black coloration is found on the top one-half to one-third of the gill branches, with no pigmentation on the apices on the paler colored animals. The background color is translucent white. Inside the gill rachis can be seen the same flat, glandular-like structures found in other *Halgerda* species as noted in the present study and in previously described species (Gosliner and Fahey 1998).

The anal papilla is short and white in color. The wide foot, which has a white edge, extends posteriorly beyond the mantle margin. The oral tentacles are short and digitiform.

BUCCAL ARMATURE. — The buccal mass is not pigmented, and the radular sac is elongate and lies flat against the buccal bulb. The radular formula of the dissected specimen is  $43 \times 30.0.30$  (CASIZ 073272) (Fig. 8). The inner four teeth are slightly smaller than the middle lateral teeth, and all teeth are hamate. The outer three lateral teeth are fimbriate.

REPRODUCTIVE SYSTEM. — The reproductive system is triaulic (Fig. 3D). The wide ampulla is flattened and lies against the female gland mass. The female gland mass is larger than the prostate gland. The ampulla narrows into the postampullary duct, bifurcates into the vas deferens and oviduct. The short oviduct enters the female gland mass. The short vas deferens separates from the ampulla and widens into the large, two-part glandular prostate that folds onto itself. The muscular portion of the vas deferens leaves the prostate in a long, single duct with one half-loop, then widens into the short, wide penial bulb. The short uterine duct emerges from the female gland mass and joins the receptaculum seminis its base. The receptaculum duct is moderately long and joins the round receptaculum seminis with the much larger, spherical bursa copulatrix adjacent to the vagina. The prostate lies alongside the bursa, which is approximately the same size. The top of the receptaculum is partially hidden under the bursa and is also slightly tucked under the prostate. The vaginal duct, which emerges from the base of the bursa copulatrix, is long and thin. It does not enlarge at its exit adjacent to the base of the male aperture. The common genital atrium is not as wide as the penis.

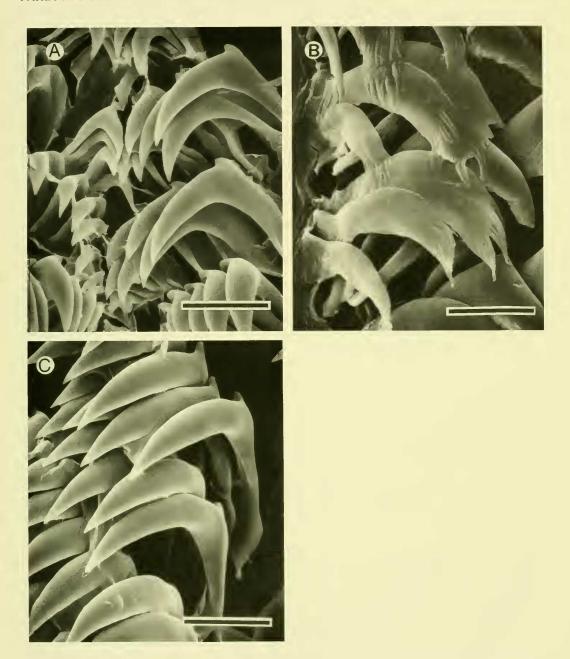


FIGURE 8, *Halgerda toliara* sp. nov. (CASIZ 073272) Mora Mora, Madagascar. Scanning electron micrographs. A. Inner lateral teeth, scale = 20 µm; B. Outer lateral teeth, scale = 15 µm; C. Middle lateral teeth, scale = 25 µm.

DISCUSSION. — Halgerda toliara shares some common characteristics with other species of the genus. It has a firm, smooth, and rigid body with a pattern of low ridges on the mantle arranged in a reticulate pattern. There are no large tubercles on the dorsum of Halgerda toliara as is common in many other members of the genus. Its body profile is relatively low like H. dalanghita and H. dichromis. There is a large gill with branchial leaves that appear to have internal glands. Halgerda

toliara has four sparsely pinnate branchia, unlike other species (e.g., *H. formosa*) with four highly pinnate branchia.

As with all other members of the genus except *Halgerda dalanghita*, *H. toliara* has an elongate radula sac. However, the sac does not protrude away from the buccal mass, but lies flat against it.

The rhinophores of most *Halgerda* are stocky at the base, and tapering at the tips, with the lamellae extending the length of the stalk. In contrast, the stalks of the rhinophores of *H. toliara* have a smooth, consistent diameter two-thirds of their length. The stalk then widens at the lamellae before tapering to the apices. In addition, *H. toliara* is unique among described species in that the rhinophore base is devoid of black pigment while the rhinophore club is entirely black. The anal papilla of some *Halgerda* has black pigmentation on either or both the posterior and anterior sides. *H.toliara* has only the white ground color.

The reproductive system of *Halgerda toliara* shares some characters, such as the round bursa copulatrix, with other *Halgerda* (*H. formosa*, *H. dalanghita*, and *H. dichromis*). The long, thin vagina is common to *H. dalanghita* and *H. albocristata* (Gosliner and Fahey 1998). The bulbous penis is common to *H. formosa* and *H. albocristata*. The prostate of other *Halgerda*, including *H. formosa* covers the bursa copulatrix (Willan and Brodie 1989; Carlson and Hoff 1993). The prostate of *H. toliara* has two parts, is long and folded and lies next to the bursa, similar to *H. dalanghita*.

There are distinct differences between *Halgerda toliara* and other *Halgerda* species with yellow-orange lined ridges. For example, there are significant reproductive anatomical differences between *H. toliara*, *H. wasinensis*, and *H. formosa*. *Halgerda toliara* has a prostate which does not cover the bursa copulatrix whereas *H. formosa* has a prostate which covers the bursa as in *H. wasinensis* (Rudman, 1978). *Halgerda toliara* has a long, thin vaginal duct that is longer than the ejaculatory duct. *Halgerda formosa* has a short vaginal duct that is much shorter than the ejaculatory duct. *Halgerda wasinensis* has a thin vaginal duct that is the same length as the ejaculatory duct. There is a muscular sphincter at the entry to the vagina in *H. formosa*, that is absent in *H. toliara*. *Halgerda wasinensis* has a muscular vagina, but no sphincter is apparent in Rudman's (1978) drawing of the reproductive system. *Halgerda formosa* has a much larger, bulbous penis than does *H. toliara*. *Halgerda formosa* also has long, fingerlike folds in the vaginal atrium, which *H. toliara* does not have in the long, thin vagina.

In addition, the radular morphology differs between the species with yellow-orange lined ridges. The inner four teeth of *H. toliara* are similar in size whereas the first 25 teeth of *H. wasinensis* are similar in size and the seven inner teeth of *H. formosa* are similar.

The external morphology differs between these species with yellow-orange ridges as well. Both *H. formosa* and *H. wasinensis* have dark markings on the notum and the foot, whereas *H. toliara* has no dark spots. *H. toliara* has small yellow tubercles along the mantle edge, and *H. formosa* has white tubercles. The gill branches of *H. formosa* and *H. wasinensis* are highly pinnate, but the gill branches of *H. toliara* are sparsely pinnate.

A discussion of generic characters has been treated by previous authors (Rudman 1978; Willan and Brodie 1989; Gosliner and Fahey 1998) and will not be repeated here.

From this study, it appears that many of the characteristics of *Halgerda toliara* are similar to other members of the *Halgerda* genus and a testable hypothesis of phylogeny is needed to determine how closely these species are related.

### **ACKNOWLEDGMENTS**

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